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Hautmann, M ; Hagdorn, H

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RESEARCH PAPER

Oysters and oyster-like bivalves from the Middle Triassic Muschelkalk of the Germanic Basin

M. Hautmann · H. Hagdorn

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Abstract Middle Triassic marine deposits of the Germanic Basin (Muschelkalk) record a significant proliferation of cementing bivalves from different families. Based on previously undescribed, excellently preserved material from the Willebadessen Member (late Anisian, Illyrian) of the Upper Muschelkalk Trochitenkalk Formation of Willebadessen (Germany), we propose the new genus *Noetlingiconcha*, type species *N. speculostreum* sp. nov., for strongly plicate prospondylids lacking auricles. The new genus differs from *Terquemia* and *Enantiostreon* in being plicate rather than costate, and from *Newaagia* in the absence of auricles. We demonstrate that *N. speculostreum* was invariably attached by its right valve, in contrast to an externally similar species from the Lower Muschelkalk Freudenstadt Formation (lower Anisian, Bithynian) that was exclusively cemented by its left valve and thus represents the geologically oldest known oyster species. Previous reports of amphi-pleurothetic cemented bivalve species from the Muschelkalk probably result from lumping together these two externally similar species. The constancy of sinistral attachment in the geologically oldest Ostreidae suggests that left-pleurothetic valve orientation was already established in the ancestry of this family. Palaeontological data are therefore in accordance with genetic and larval shell morphology analyses that identified Pterioidea as the sister taxon of Ostreoidea, because Pterioidea contains several Permian-Triassic genera with an anatomically lower left valve.

Keywords Bivalvia · Ostreidae · Prospondylidae · Triassic · Taxonomy · Evolution

Kurzfassung Im Muschelkalk (Mitteltrias, Anisium-Ladinium) des Germanischen Beckens kommt eine Vielzahl zementierender Muschelarten aus unterschiedlichen Familien vor, deren stammesgeschichtliche Beziehungen umstritten sind. Auf Grundlage von außergewöhnlich gut erhaltenem Material aus dem Willebadessen-Member (spätes Anisium, Illyrium) der Trochitenkalk-Formation wird in der Familie Prospondylidae die neue Gattung *Noetlingiconcha*, Typusart *N. speculostreum* sp. nov., aufgestellt, die aurikellose Arten mit stark gefaltetem Schalenrand umfasst. Die neue Gattung unterscheidet sich von *Terquemia* und *Enantiostreon* durch die Verfaltung der Klappenränder und von *Newaagia* durch das Fehlen von Aurikeln. *N. speculostreum* war ausschließlich rechtsseitig festgewachsen, im Gegensatz zu einer äußerlich ähnlichen Art aus der Freudenstadt-Formation (unteres Anisium, Bithynium) des Unteren Muschelkalks, die ausschließlich linksseitig aufgewachsen war und somit die erdgeschichtlich älteste bekannte Austernart darstellt. Frühere Berichte über das Vorkommen einer austerähnlichen Art im Muschelkalk, bei der sowohl links- als auch rechtsseitige Anheftung vorgekommen sein soll, resultieren vermutlich aus der Vermischung dieser beiden äußerlich ähnlichen Arten. Die Konstanz linksseitiger Aufwachsung bei den stammesgeschichtlich ältesten Austern weist darauf hin, dass dieses Merkmal bereits in der Vorfahrenschaft der Ostreidae entwickelt war. Als möglicher Kandidat kommen die Pterioidea in Frage, bei denen mehrere permotriassische Taxa ebenfalls eine anatomisch untere linke Klappe

M. Hautmann (✉)
Paläontologisches Institut und Museum, Karl Schmid-Strasse 4, 8006 Zürich, Switzerland
e-mail: michael.hautmann@pim.uzh.ch

H. Hagdorn
Muschelkalkmuseum Ingelfingen, Schloss-Str. 11, 74653 Ingelfingen, Germany

besaßen und die bereits durch Larvalschalenuntersuchungen und molekularbiologische Analysen als mögliche Schwestergruppe der Ostreidae identifiziert worden sind.

Schlüsselwörter Muscheln · Ostreidae · Prospondylidae · Trias · Taxonomie · Evolution

Introduction

Identification of the geologically earliest Ostreidae (oysters) has always challenged palaeontologists for two reasons. First, the cemented mode of life results in irregular shell morphologies that oysters share with other cementing bivalve families (e.g., Newell and Boyd 1970). Second, information on muscle scars and ligament morphology is mostly lost because of diagenetic dissolution of the originally aragonitic inner shell layer that characterizes early representatives of the family (Hautmann 2001a, b, 2006a; Carter and Malchus in Carter et al. 2011). Paradigmatic for these problems are the cementing bivalves from the Middle Triassic Muschelkalk of the Germanic Basin. Early authors have placed them indifferently in *Ostrea* or *Ostracites* until Noetling (1880) demonstrated that specimens that he identified as *Ostracites cristadifformis* Schlotheim, 1820 and *Ostrea complicata* Goldfuss, 1833 were attached by their right valves and thus no oysters. Noetling (1880) transferred these species to *Terquemia*, but Philippi (1898, p. 619) pointed out that they are distinguished from this genus by the broad resilifer, as figured in Noetling (1880), and the very coarse "ribs" (= plicae). Bittner (1901a) explicitly referred to Philippi's (1898) observations when he introduced the genus *Enantiostreon* ("mirrored oyster") for oyster-like species attached by the right valve. However, he also stated that his new species *E. hungaricum*, which is the type species of *Enantiostreon* by the subsequent designation of Diener (1923), was not closely allied to the species from the Germanic Muschelkalk. Nevertheless, most subsequent authors (e.g., Frech 1909; Assmann 1915; Diener 1923; Schmidt 1928) followed Bittner (1901a) and placed all plicate oyster-like species from the Germanic Triassic in *Enantiostreon*, whereas other cementing bivalve species have been referred to *Philippiella* Waagen, 1907 (= *Newaagia* Hertlein, 1952) and *Placunopsis* Morris and Lycett, 1853. In consequence, the presence of oysters in the Middle Triassic was generally disputed (Philippi 1898). This view was revised again when Seilacher (1954) noted exceptions from Noetling's (1880) observation. In the absence of muscle scar impressions, Seilacher (1954) used the following criteria for distinguishing between right and left valves: (1) life position, (2) prevalently retrocrescent shell growth (as already used by Bittner 1901a), and (3) differences in shell height between the anterior and posterior margin. Seilacher (1954) thereby identified invariably sinistrally cemented *Lopha*-like specimens fixed to the shell exterior of the limid bivalve *Plagiostoma lineatum* from the Lower Muschelkalk Freudenstadt Formation. He concluded that these specimens were true oysters and accordingly that cementing bivalves previously united in the same species (*Ostracites cristadifformis*) actually belong to different families. An alternative possibility was suggested by Cox (1969, p. *N*380), who proposed that *Ostracites cristadifformis* might have been attached by the left or right valve indifferently. This, in addition to an allegedly oyster-like resilifer and some similarity in the rib pattern, has made *Ostracites cristadifformis* a candidate ancestor of "true," exclusively sinistrally attached oysters and a possible link between oysters and the geologically older Prospondylidae (Márquez-Aliaga et al. 2005).

Apart from being attached by the left valve, Ostreidae have additional shell characters that distinguish them from other cementing bivalves (Hautmann 2006b). Most important in the context of the material discussed below is the alivincular-arcuate ligament condition (Hautmann 2004), i.e., an elevated resilifer of the right valve and bulge-like bourrelets of the left valve articulating with opposing depressions. Additionally, oysters lack a pallial line (Stenzel 1971), and the myostracum of the right valve may form a conspicuous elevation in some oyster species, a feature that to our knowledge has not been observed in other bivalve families.

Material

As noted above, the aragonitic inner shell layer of cementing bivalves and thus all these characters are usually not preserved in the Muschelkalk. However, two notable types of exceptions occur: (1) original shells were completely dissolved, resulting in voids that show detailed impressions of the original internal and external surfaces; for this preservation, diagenetic consolidation and cementation of the sediment prior to dissolution of aragonitic and calcitic shell layers were required; (2) the same process plus subsequent secondary recrystallization of such voids either by calcite cement or by dolomite. For diagenetic pathways of bioclasts in the Muschelkalk, see Bachmann (1973), Lukas (1992), and Zeeh and Hagdorn (2002). The latter type of preservation typically occurs in shallow water oolitic sediments. Where such sediments had been influenced by humic acids in karstified areas, the oolites were dissolved, and the sediment became soft and friable enough to allow mechanical preparation. A good deal of the Muschelkalk bivalve and gastropod diversity was described from sediments yielding such recrystallized specimens (in

German "Ersatzschalen-Lagerstätten"), which gained early interest among palaeontologists.

A detailed taphonomical analysis of the material is beyond the scope of this article, but coarse sparry calcite crystals originating from the outer and inner shell surfaces suggest that the specimens under study are preserved with a replacement shell, mineralized in voids after dissolution of the original shell (preservation type 2 described above). However, the preservation of phoronoid shell borings (*Talpina, Calciroda*) and acrothoracian barnacles (*Rogerella*) in some specimens appears incompatible with this mode of preservation and might indicate micrite seams covering primary surfaces (Zeeh and Hagdorn 2002) or in situ recrystallization of the shells.

The material of Noetling (1880) stems from a small quarry near Großhartmannsdorf (Lower Silesia; now Racibórowice, Poland) that exposed the "Wehrauer Schichten", strata equivalent to the Terebratelbank Member of the Lower Muschelkalk Jena Formation in Germany (Anisian, Pelsonian to early Illyrian). Because of strong weathering of the sediment, the calcitic replacement shells could be isolated from the matrix and displayed most diagnostic characters.

The material under study was derived from another exceptional lagerstätte of this type, the Upper Muschelkalk "Astartebank" (*Astarte* bed) at the top of the Willebadessen Member of the Trochitenkalk Formation (late Anisian, late Illyrian; *robustus* biozone) of the Egge Hills around Willebadessen (Nordrhein-Westfalen, Germany; Fig. 1). It was Roemer (1851) who realized the extraordinary preservation of bivalves in this lagerstätte and described some new taxa, among them *Ostrea willebadessensis*, an incompletely preserved shell of a large bivalve devoid of costae or plicae with a long and straight hinge area, and a sharply delineated, triangular resilifer. Despite of its incomplete preservation, this bivalve can be assigned to *Newaagia*, a genus fairly common in the Astartebank. More than a century later, Busse (1972) reported a total of 82 species from the Astartebank in this area, with a clear dominance of bivalves. According to Hagdorn (in preparation), the Astartebank contains a mixed assemblage derived from two palaeocommunities that inhabited the solid frames of bivalve-crinoid bioherms and the coarse-grained oolitic and biogenic sediments in between the bioherms. Similar bioherms of slightly older age (Crailsheim Member of the Trochitenkalk Formation, *atavus* biozone) were described in detail by Hagdorn (1978) and Hagdorn and Ockert (1993). Primary frame builders were oyster-like bivalves with strongly plicate or costate shells that were hitherto assigned to *Enantiostreon cristadifforme* or *Newaagia noetlingi*, respectively. However, due to their "normal" Muschelkalk preservation, the hinge-ligament complex of these cementing bivalve species is obscured.

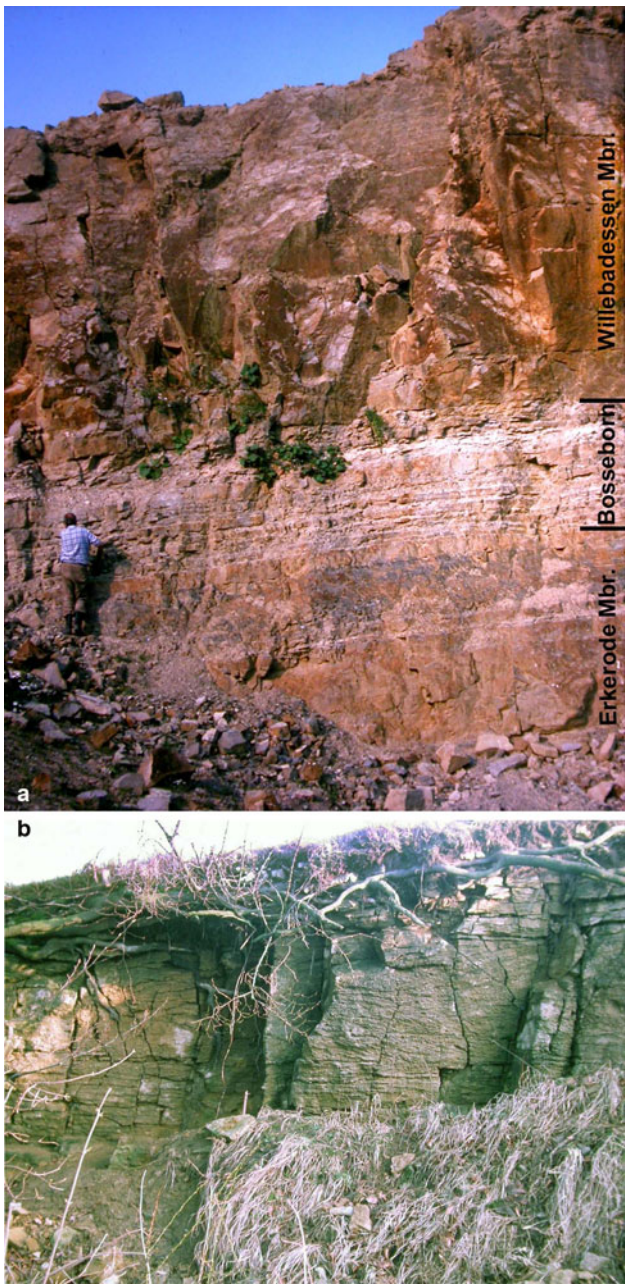


Fig. 1 Outcrops of the Upper Muschelkalk Trochitenkalk Formation in Nordrhein-Westfalen. **a** Niesen quarry with thick-bedded shallow water oolites of the Willebadessen Member; the Astartebank, which yielded the material under study, is at the top of this member. For locality data, see Röhl (1988). **b** Abandoned Altenheerse quarry with crinoidal limestones of Astartebank. Locality photos 1978

Our study is based on material collected by H.H. since 1976 basically in the localities previously reported by Busse (1972), to which it is referred for further geographical details. The main suite of fossils (series MHI 943) is from locality IX of Busse (1972), an abandoned quarry near the cemetery of Altenheerse north of

Willebadessen (Fig. 1). There, the Astartebank formed the floor level of the quarry, which provided excellent conditions for quantitative collecting because the sediment was strongly weathered and friable. After wettening, sediment remains could be easily removed from the replacement shells. Nowadays, the quarry is completely covered with vegetation and overbuilt.

In the context of this article, we concentrate on specimens that externally resemble the holotype of *Ostracites cristadifformis* (Fig. 2a), but that additionally show internal shell characters that allow their precise taxonomic characterisation. The original illustrations of taxa erected by von Schlotheim (1820), Münster (in Goldfuss 1833), Goldfuss (1833), Giebel (1856), and Noetling (1880) that are discussed in the taxonomic part of this paper are reproduced in Figs. 2 and 3. The new material herein described is housed in the Muschelkalkmuseum Ingelfingen (MHI).

New morphological data

We have examined a suite of conspecific specimens that externally resemble *Ostracites cristadifformis* (Fig. 2a) but additionally show details of the shell interior, allowing identification of the following main characters (Fig. 4): (1) an exclusively dextral attachment, (2) an alivincular-areate ligament area, with flat bourrelets and a deep and narrow resilifer that becomes broad only in late ontogenetic stages, (3) the absence of auricles, (4) a single large adductor muscle scar, and (5) a strongly plicate shell margin. Because orientation and ligament morphology are key characters for distinguishing Ostreidae and Prospondylidae, they are discussed in more detail in the following.

Pleurothetic orientation

In spite of their diagenetic history, some specimens (Fig. 4a, d) show traces of the adductor muscle attachment, which allows distinction between the left and right valve because the adductor muscle is located in the posterior part of the shell in all monomyarian pteriomorphs. As additional though less rigorous criteria for left/right identification of the valves, we used the prevalently retrocrescent shell growth and the higher elevation of the anterior shell margin (Seilacher 1954). As shown in Fig. 4, all attached valves in our sample where at least one of these characters is observed are right valves (Fig. 4a, d–e, g, i, m–n), which excludes that this species belongs to the Ostreidae. The consistently dextral attachment is also at variance with the hypothesis of indifferent attachment in this species (Cox 1969).

Ligament area

In addition to shell orientation, ligament morphology is an important character for distinguishing Ostreidae from morphologically convergent bivalves belonging to other cementing bivalve families such as the Prospondylidae (Hautmann 2004). Ostreidae have a resilifer that is broad in relation to the bourrelets and that is asymmetrical between the valves, forming a boss-like elevation in the right valve that fits into a corresponding depression of the left valve (e.g., Newell and Boyd 1970, fig. 8; Hautmann 2006b, fig. 2). Conversely, the bourrelets of the left valve form an anterior and posterior bulge fitting into concave counterparts of the opposite valve. This asymmetrical ligament area has been termed *alivincular-arcuate* by Hautmann (2004). It is clearly different from the *alivincular-areate* ligament type in Prospondylidae, where the bourrelets of both valves are flat and much broader than the resilifer, which is never convex (Hautmann 2004). Within the Prospondylidae, there is still some variation of the ligament, with the tendency of narrowing and deepening the resilifer (Hautmann 2001a, b).

The invariance of the alivincular-arcuate ligament condition in the Ostreidae was doubted by Checa et al. (2006), who cited some counter examples of the Gryphaeidae. However, it was clearly stated in Hautmann (2004, p. 168) that Gryphaeidae have an alivincular-areate ligament area and in this respect differ from Ostreidae, lending some credence to the hypothesis of a diphyletic origin of Ostreoidea (Stenzel 1971). Confusion also was raised by the fact that perception of elevation and depression in photographs of the ligament area is subjective, leading occasionally to a reversal of the true relation (see Hautmann 2006b, p. 669). We acknowledge that the morphology of the ligament area in Ostreidae, like any other structure, is subject to intraspecific variation and to modifications during evolution, and that an occasional return to the atavistic alivincular-areate condition is not excluded. However, we affirm that the described asymmetry between the ligament area of the left and right valve occurs in all Triassic Ostreidae in which this character is sufficiently known (e.g., '*Ostrea*' *montiscaprilis* Klipstein, 1843 (see Bittner Bittner 1901a, pl. 6, figs 14-18), *Umbrostrea emamii* Hautmann, 2001a, *U. iranica* Hautmann, 2001a, '*Alectryonia*' *parasitica* Krumbeck, 1913, and *Nacrolopha carolae* Carter and Malchus [in Carter et al. (2011), which suggests that the alivincular-arcuate ligament condition is a primitive character of Ostreidae.

Ligament morphology is perfectly preserved in some of our specimens (Fig. 4a–b, f, h–i, k, m). The width of the ligament area is typically moderate (e.g., Fig. 4b, h), but some specimens also developed relatively broad areas (Fig. 4i, m), possibly in response to substrate morphology.

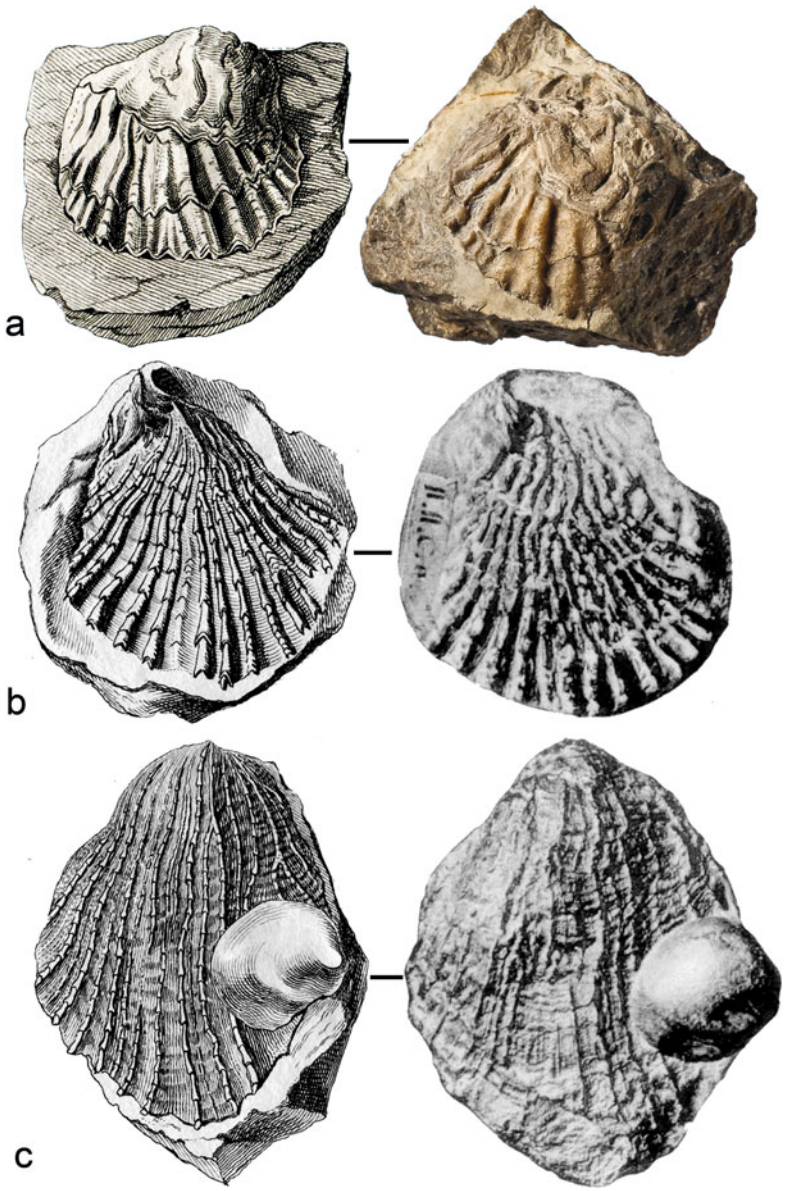
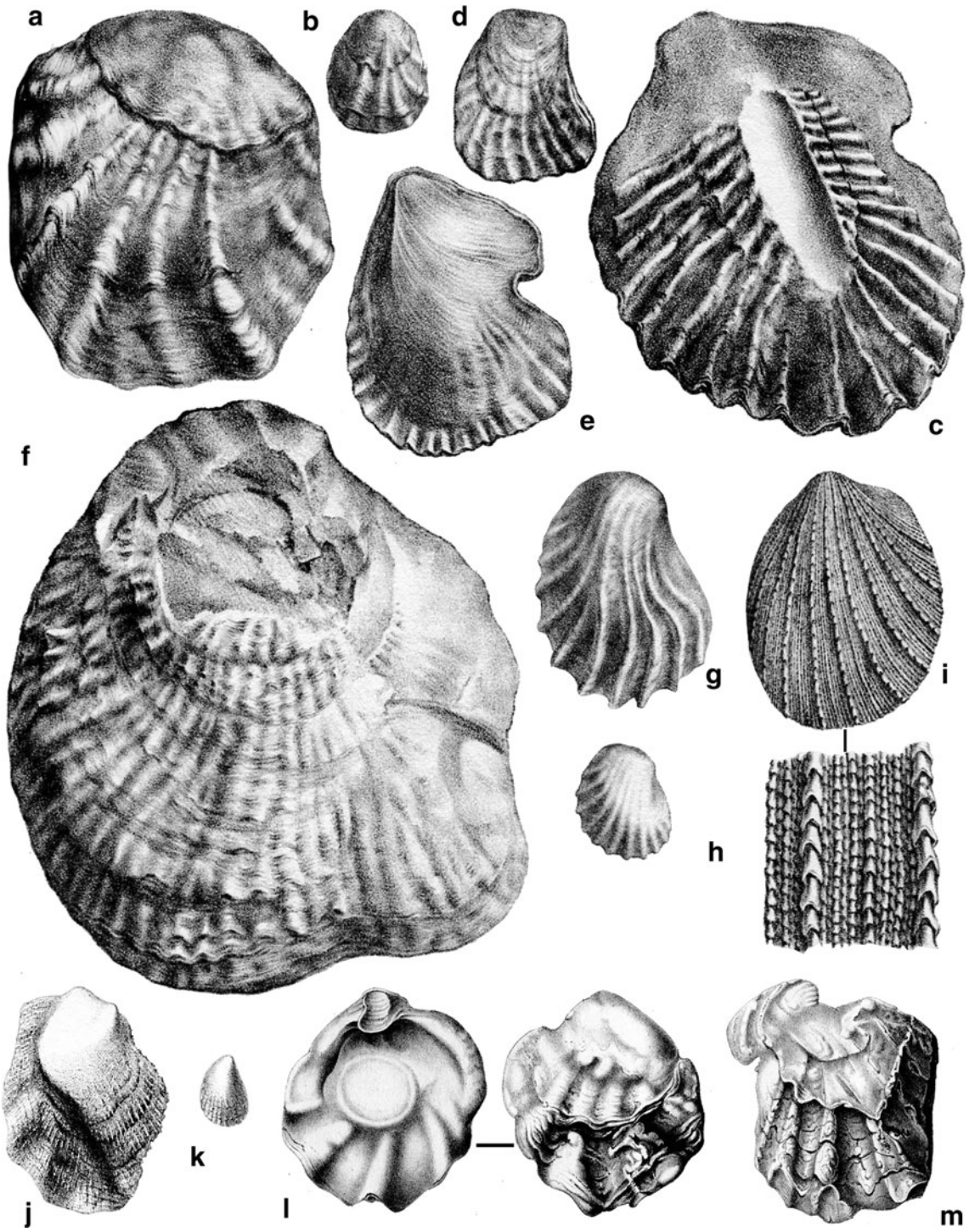


Fig. 2 Originals of Schlotheim (1823) plate 36 (collection of the Museum für Naturkunde, Berlin). **a** *Ostracites crista difformis* Schlotheim, 1820, p. 245, Schlotheim 1823, p. 111; pl. 36, fig. 2; "Muschelflötzkalk, Gegend von Weimar" (Muschelkalk beds near Weimar); holotype, MB.M.5555. **b** *Ostracites spondyloides* Schlotheim, 1820, p. 239; Schlotheim 1823, p. 111, pl. 36, Fig. 1b; Upper Muschelkalk, Weimar; photography after Philippi and Frech 1903, pl. 4, Fig. 1; lectotype, designed herein. **c** *Ostracites spondyloides* Schlotheim, 1820, with epizoic *Ostracites sessilis*, p. 239; Schlotheim 1823, p. 111, pl. 36, Fig. 1a; Upper Muschelkalk, Lossberg near Tonna; photography after Philippi & Frech 1903, pl. 4, fig. 3. All figures ×1

The height of the ligament area also varies from large to moderate, but examples of moderate height may have been caused at least partly by erosion of the distal (ontogenetic older) part during the lifetime of the individual. Notwithstanding the variability in size, the bourrelets are always flat, divided by a deep and initially narrow resilifer that becomes broader in late ontogenetic stages. The resilifer is concave in both valves (Fig. 4b, f, h, m for right valves, Fig. 4k for a left valve). Hinge teeth are lacking. The described morphology of the ligament area is alivincular-areate and typical of Prospondylidae (Hautmann 2001a, b). Some of our specimens closely resemble *Terquemia* Tate, 1868 in this respect (Fig. 4b, h), whereas others (e.g., Fig. 4m) are more similar to *Newaagia*.

Taxonomic affiliation

Dextral cementation and ligament morphology unambiguously indicate that the specimens discussed above belong



to the family Prospondylidae (see revised family diagnosis in Hautmann 2001a). Based on the great morphological similarity, we assume that our material is conspecific or at least congeneric with the specimens that Noetling (1880) assigned to *Terquemia cristadifformis* and *T. complicata* (regarded as synonyms by Assmann 1915). This has important bearings because Fig. 1a in Noetling (1880) (reproduced in Fig. 3l herein) apparently shows an oyster-like resilifer (Philippi 1898, p. 617), and this feature has entered the diagnosis of *Enantiostreon* (Cox 1969; Hautmann 2001a) since Noetling's material has been assigned to this genus (Bittner 1901a). The allegedly oyster-like resilifer has also contributed to consideration of *Ostracites cristadifformis* as a candidate ancestor of Ostreidae, as

◄ **Fig. 3** Originals of Goldfuss (1833), Münster in Goldfuss (1833), Giebel (1856), and Noetling (1880). **a** *Ostrea difformis* Schlotheim, "upper" valve of adult specimen, Goldfuss 1833, pl. 72, fig. 1a. **b** *Ostrea difformis* Schlotheim, "upper" valve of juvenile specimen, Goldfuss 1833, pl. 72, fig. 1b. **c** *Ostrea complicata* Goldfuss, 1833, "upper" valve, Goldfuss 1833, pl. 72, fig. 3a. **d** *Ostrea complicata* Goldfuss, 1833, "upper" valve of juvenile specimen, Goldfuss 1833, pl. 72, fig. 3c. **e** *Ostrea complicata* Goldfuss, 1833, "lower" valve, Goldfuss 1833, pl. 72, fig. 3b. **f** *Ostrea multicostata* Münster in Goldfuss, 1833, "upper" valve, Goldfuss 1833, pl. 72, fig. 2. **g** *Ostrea decemcostata* Münster in Goldfuss, 1833, "lower" valve of adult specimen, Goldfuss 1833, pl. 72, fig. 4a. **h** *Ostrea decemcostata* Münster in Goldfuss, 1833, "lower" valve of juvenile specimen, Goldfuss 1833, pl. 72, fig. 4b. **i** *Ostrea comta* Goldfuss, 1833, "lower" valve, Goldfuss 1833, pl. 72, fig. 6a,b. **j** *Ostraea scabiosa* Giebel, 1856, Lower Muschelkalk, Lieskau, Giebel 1856, pl. 2, fig. 17. **k** *Ostraea liscaviensis* Giebel, 1856, Lower Muschelkalk, Lieskau, Giebel 1856, pl. 2, fig. 2. **l** *Terquemia complicata* (Goldfuss, 1833), left valve, internal and external view, Lower Muschelkalk, Großhartmannsdorf, Noetling 1880, pl. 8, fig. 1a-b. **m** *Terquemia difformis* (Schlotheim, 1820), right valve, external view, Lower Muschelkalk, Großhartmannsdorf, Noetling 1880, pl. 8, fig. 1a-b. All figures × 1. Figs a-i have been drawn without use of a mirror and are thus mirror-inverted (teste Goldfuss 1863, p. 2, footnote)

explicitly stated in Márquez-Aliaga et al. (2005, p. 130). However, Noetling (1880, p. 321) noted that the ligament pit (= resilifer) was fairly narrow, in apparent contradiction to his figure of this structure. By comparison with our material, we conclude that Noetling (1880) has figured a specimen in which only the ontogenetically youngest, relatively broad part of the resilifer is preserved, whereas the narrow dorsal part of the resilifer and much of the lateral part of the bourrelets were eroded. Broadening of the resilifer during ontogeny is clearly visible in some of our specimens (e.g., Fig. 4h), and erosion of the peripheral parts of the ligament area is observed where this part was not protected by the substrate on which the specimen was cemented (e.g., Fig. 4n). As a result of such an incomplete preservation, Noetling's (1880, fig. 1a) specimen shows a resilifer that is broad in relation to the (eroded) bourrelets. The oyster-like appearance of the ligament area in Noetling (1880, fig. 1a) is thus interpreted as a preservation artefact.

Without knowledge of the internal shell characters described above, "*Enantiostreon cristadifforme*" was used as a collective name for plicate oyster-like shells of the Germanic Muschelkalk until Seilacher (1954) suggested that this procedure has united at least two species from different families (Ostreidae and Prospondylidae). We have re-studied Seilachers (1954) material from the Freudenstadt Formation (early Anisian, Bithynian) of the Black Forest (refigured in Hautmann 2006a, fig. 1) and similar material from the same formation in the collection of the MHI (Fig. 5), which are small plicate shells attached to the shell exterior of *Plagiostoma*. We confirm Seilacher's (1954) observation that these shells were invariably sinistrally attached and thus belong to a different family than the herein described material from Willebadessen. From this observation a major taxonomic problem arises, because the holotype of *Ostracites cristadifformis* shows no internal characters and no clear indication of valve orientation (Fig. 2a). Contrary to Márquez-Aliaga et al. (2005), it is also uncertain whether it is an attached or free valve, because the strongly eroded shell visible in the dorsal part of the specimen may equally represent an attachment substrate for *O. cristadifformis* or another cementing bivalve settling on *O. cristadifformis*. Given the inadequateness of its holotype, *O. cristadifformis* must be regarded as a nomen dubium.

Also the generic assignment of the specimens from Willebadessen is problematic. They agree with *Terquemia* in the ligament morphology and the lack of auricles, but the shell of *Terquemia* is costate and not plicate (e.g., Newell and Boyd 1970, p. 223). Nothing is known of the shell interior of the type species of *Enantiostreon*, but externally it also differs in having a costate rather than a plicate shell (Fig. 6). *Dentiterquemia* Hautmann and Golej, 2004 is plicate but is unique in having a series of small teeth on the hinge margin. *Newaagia* differs in the generally broader and shallower resilifer, the costate shell, and the presence of auricles (Fig. 7). Because no appropriate names are available, the introduction of a new genus and species for the herein presented material is required (see systematic description chapter).

Phylogenetic implications

Ostracites cristadifformis has previously been regarded as a collective name for plicate cementing bivalves from two different families (i.e., Ostreidae and Prospondylidae; Seilacher 1954), or alternatively as a species that cemented with the right or left valve indifferently (Cox 1969). Our observations are in favour of the first hypothesis, because a suite of clearly conspecific specimens from the same bed at the Willebadessen locality are invariably dextrally attached, in accordance with the morphology of their ligament area, which indicates a prospondylid rather than ostreid affiliation. In contrast, externally similar bivalve epizoans on the limid bivalve *Plagiostoma* from the Freudenstadt Formation are invariably sinistrally attached, as already observed by Seilacher (1954). This does not exclude the theoretical possibility that additionally an amphi-pleurothetically attached cemented bivalve species existed in the Germanic Basin, but this hypothesis cannot be tested on the basis of the material described by Márquez-Aliaga et al. (2005) that mostly shows little indication of left/right orientation, let alone taxonomically important details such as ligament area and muscle impressions. With the current state of knowledge, we thus reject the presence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◄ **Fig. 4** *Noetlingiconcha speculostreum* gen. et sp. nov. (collection of the Muschelkalkmuseum, Ingelfingen). MHI 943/1, *right* valve cemented on two shell fragments of the same species; **a**, holotype, view of shell interior, showing outline, large, round adductor muscle scar (*arrow*), plicate shell margin and ligament area, ×1; **b** details of ligament area, note flat bourrelets and deep and narrow resilifer, ×2; **c** shell exterior, showing ornament and cementation of the holotype (individual on the right) on two shell fragments, ×1. MHI 943/14, *right valve*, **d** interior, showing adductor muscle scar (*arrow*), **e** exterior, showing plicate shell margin and cementation on shell fragment; ×1. MHI 943/13, *right valve*, **f** ligament area, **g** shell exterior, showing ornament and cementation on shell fragment; ×1. MHI 943/6, *right* valve cemented on *Newaagia noetlingi*, **h** detail of ligament area, note flat bourrelets and ventral broadening of resilifer, ×2, **i** shell interior, ×1. MHI 943/2, *left valve*, **j** shell exterior, showing xenomorphic area and bi- and trifurcating plicae, ×1, **k** ligament area, ×2. **l** MHI 943/11, exterior of right valve, showing ornament and flat attachment area, ×1. MHI 943/9, right valve, **m** interior, **n** exterior showing cementation on shell fragment, ×1

Fig. 5 *Umbrostrea* sp., collection of the Muschelkalkmuseum Ingelfingen, MHI 2081, five specimens settling on the posterior (anatomically upper) shell margin of the limid *Plagiostoma*. Note that valve curvature indicates cementation by the left valve for all specimens. Also note dissolution of the inner shell layer, leading to the non-preservation of hinge details. *Scale bar* represents 1 cm

of such an "ambivalently" (amphi-pleurothetic) attached cementing bivalve species in the Germanic Muschelkalk as a phylogenetic link between Ostreidae and the geologically older Prospondylidae (Márquez-Aliaga et al. 2005), a hypothesis that probably arose from lumping together externally similar species from either family. It should also be noted that all established examples for amphi-pleurothetic attachment in cementing bivalves concern taxa with orthothetic ancestors, such as the heterodont bivalve families Chamidae Lamarck, 1809 and Diceratidae Dall, Dall 1895, and the freshwater bivalve family Etheriidae Deshayes, 1832. The hypothesis of ambivalent attachment as an intermediate state between sinistrally attached Ostreidae and a pleurothetic ancestor with the opposite (dextral) orientation (Prospondylidae) is therefore not conclusive. The remarkable constancy of sinistral attachment in the earliest known Ostreidae rather suggests that this family stems from a taxon in which sinistral orientation was already established. In this respect, the fossil record supports genetic analyses that identified Pterioidea as the sister group of oysters (e.g., Steiner and Hammer 2000; Giribet and Wheeler 2002; Giribet and Distel 2003; Matsumoto 2003), because several Permian-Triassic pterioid taxa have an anatomically lower left valve (e.g., Bakevelliidae, Cassianellidae; for examples of sinistral orientation in different genera of these families, see Fürsich and Wendt 1977; Seilacher 1984; Muster 1995; Aberhan and Muster 1997). Moreover, Ostreidae agree with the pterioid family Bakevelliidae in several larval shell characters, most notably in an opisthogyrate larval shell coiling that possibly indicates a basal dichotomy in pteriomorphian bivalves (Malchus 2004).

Systematic palaeontology

Family Prospondylidae Ptschelinceva, 1960
Genus *Noetlingiconcha* gen. nov.

Type species: *Noetlingiconcha speculostreum* sp. nov.

Derivation of name: Named for Fritz Noetling, who was the first to note dextral cementation in oyster-like species of the Germanic Muschelkalk.

Diagnosis: Shell strongly plicate, cemented to hard substrates by the right valve. Auricles absent, indicating the lack of a juvenile byssate stage preceding cementation. Ligament area alivincular-areate, relatively high in right valve, with a deep and narrow resilifer located in a central position, occasionally broadening in ventral direction. Monomyarian, with a nearly circular muscle scar located dorsal of and posterior to the center of shell.

Remarks: The strongly plicate shell distinguishes the new genus from *Terquemia*, which is costate but otherwise similar.

Noetlingiconcha speculostreum sp. nov.
?1880 *Terquemia difformis* [sic] Schlotheim—Noetling: 322, pl. 8, fig. 1.
?1880 *Terquemia complicata* Goldfuss—Noetling: 322, pl. 8, fig. 2.

Derivation of name: Combination of speculum (Latin) = mirror and ostreum (Latin) = oyster (noun in apposition). We have chosen a Latin translation of the genus name *Enantiostreon* in recognition of the traditional taxonomic treatment of this species.

Diagnosis: As for the genus.

Holotype: MHI 943/1 (Fig. 4a–c) from abandoned quarry near the cemetery of Altenheerse north of Willebadessen (Westfalia), outcrop IX in Busse (1972, p. 112).

Stratum typicum: Astartebank, Willebadessen Member of Trochitenkalk-Formation, *robustus* zone (late Illyrian, late Anisian).

Description: Medium-sized cementing species with variable size of attachment surface and corresponding xenomorphic area, depending on size and morphology of substrate. Valves retrocrescent, generally higher than long, irregular to asymmetrical drop-shaped in outline. Shell margin outside attached/xenomorphic area strongly plicate. Amplitude of plicae tends to decrease from anterior to posterior side. Plicae mostly simple but occasionally also bi- or trifurcating, varying in number from 10 to 15 in the type series. Ligament area variable in size but mostly high and relatively short, with a deep central resilifer becoming broader in ventral direction. Single large adductor muscle scar circular to subcircular in outline, its center located in the posterior and upper half of the shell.

Occurrence: Specimens with calcitic replacement shells preserving all diagnostic characters occur in (1) the Upper Muschelkalk, Trochitenkalk Formation,Willebadessen Member (Eggegebirge, Nordrhein-Westfalen) and Marbach Member (eastern margin of Black Forest, Baden-Württemberg), both members of late Anisian, late Illyrian *robustus* biozone; (2) the Lower Muschelkalk, Wehrau Beds [Noetling 1880; = Unit E of Chrząstek (2002), corresponding to the late Pelsonian (*Decurtella decurtata* biozone) Terebratelbank Member of the Jena Formation, North Sudetic Depression, Lower Silesia, Poland]. Specimens superficially resembling *N. speculostreum* are abundant as frame builders in crinoid-bivalve bioherms of (1) the Upper Muschelkalk (late Anisian, late Illyrian, *flexuosus* to *atavus* biozones) Erkerode, Crailsheim, and Hassmersheim Members of the Trochitenkalk Formation (Germany, eastern France); (2) in the Lower Muschelkalk (Anisian, Pelsonian, *Decurtella decurtata* biozone) Dziewkowice Formation of Upper Silesia, Poland (Niedźwiedzki 2000, corresponding to the Terebratelbank Member of the Jena Formation).

Remarks: Many poorly preserved oyster-like specimens that have previously been described as *Ostracites cristadifformis* (see summary in Diener 1923; Kutassy 1931) probably belong to *Noetlingiconcha speculostreum*, but the state of preservation usually does not allow definite discrimination of these specimens from co-occurring plicate oysters. As demonstrated above, this also applies to the holotype of *O. cristadifformis*, which does not show any characters that are required for its identification as either a prospondylid or an ostreid species (e.g., ligament morphology, position of adductor muscle). The only exception is the material figured by Noetling (1880) as *Terquemia difformis* and *T. complicata* (reproduced in Fig. 3l–m). These specimens differ from our material in having a lower number of plicae, but they are otherwise very similar. We provisionally include them in synonymy of *Noetlingiconcha speculostreum*, subject to clarification of the intraspecific variability of the number of plicae by means of additional material.

Ostrea complicata Goldfuss, 1833, *O. decemcostata* Münster in Goldfuss, 1833, and *O. liscaviensis* Giebel, 1856 have been placed in synonymy of *O. cristadifformis* (Assmann 1915; Schmidt 1928), but all of these species have poorly preserved types without any diagnostic features apart from their ornamentation, which however is insufficient for resolving the taxonomic problems outlined above (see reproductions of the original figures in Fig. 2c–e, g–h, k). In consequence, we regard them as nomina dubia. Although we regret abandoning well-established names, agreement on the scope of a species can only be reached on the basis of type material that shows a sufficient set of shell morphological characters. We therefore suggest *Noetlingiconcha speculostreum* as a new species name on the basis of the well-preserved material described above.

Genus *Enantiostreon* Bittner, 1901

Type species: *Enantiostreon hungaricum* Bittner, 1901a, by subsequent designation (Diener 1923) (Fig. 6).

Remarks: The lack of knowledge on internal shell characters of the type species due to dissolution of the inner shell layer (Fig. 6h, j) makes this genus doubtful. It may represent a younger synonym of *Terquemia*, based on the costate shell and the lack of auricles. Alternatively, it has been suggested that *Enantiostreon hungaricum* belongs to the Plicatulidae (Márquez-Aliaga et al. 2005). Unless new morphological information becomes available, it is suggested to avoid the use of this genus name.

Genus *Dentiterquemia* Hautmann and Golej, 2004

Type species: *Terquemia* (*Dentiterquemia*) *eudesdeslongchampsi* Hautmann and Golej, 2004.

Remarks: This genus was introduced as a subgenus of *Terquemia*. However, it differs from *Terquemia* not only in its hinge structure, as discussed by Hautmann and Golej (2004), but also in having a plicate shell. It may thus be more closely related to *Noetlingiconcha*. However, in the absence of intermediate taxa, we suggest raising *Dentiterquemia* to the genus rank, thus avoiding an unwarranted phylogenetic hypothesis.

Genus *Newaagia* Hertlein, 1952 (pro *Philippiella* Waagen, 1907)

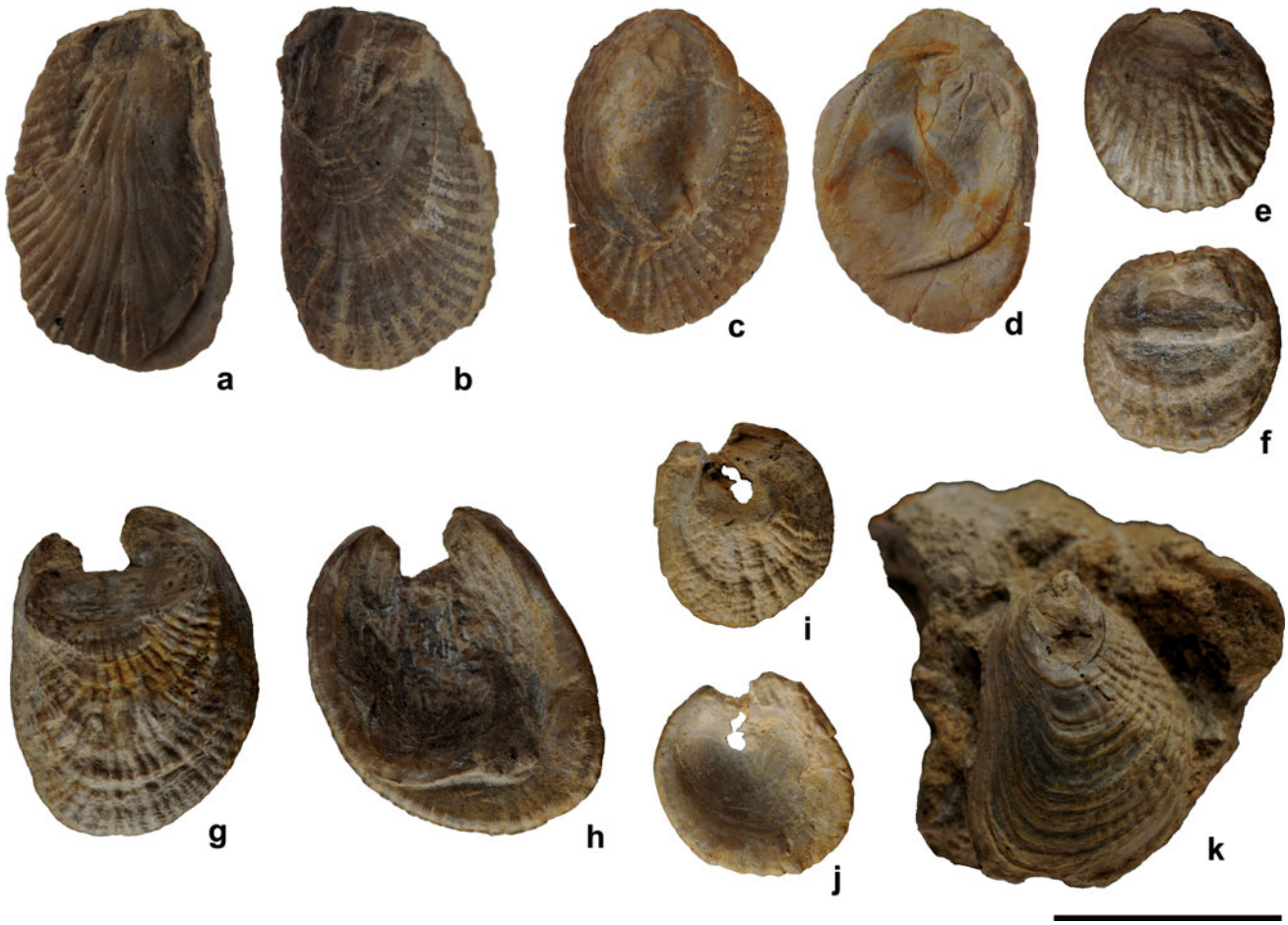

Fig. 6 Type series of *Enantiostreon hungaricum* Bittner, 1901a, b (collection of the Hungarian Geological Institute, Budapest). T. 1887, original of Bittner (1901, pl. 6, fig. 23), specimen with conjoined valves, **a** left valve, **b** right valve. T. 1888, original of Bittner (1901, pl. 6, fig. 24), right valve attached to bivalve shell, **c** exterior, **d** interior with another cementing bivalve in center of shell. T. 1231, original of Bittner's (1901, pl. 6, fig. 26) var. *inversa*, in which the left valve is more convex than the right valve, specimen with conjoined valves, **e** left valve, **f** right valve with large attachment area. T. 1153, original of Bittner (1901, pl. 6, fig. 22), right valve, **g** exterior, **h** interior, note dissolution of the inner shell layer and corresponding non-preservation of the ligament area; also note crenate shell margin but absence of plicae. T. 1236, original of Bittner's (1901, pl. 6, fig. 25) var. *subcircularis*, characterized by subcircular outline, right valve, **i** exterior, **j** interior with dissolved inner shell layer. **k** T. 1208, original of Bittner's (1901, pl. 6, fig. 20) var. *semicostata* in which the radial ribs are confined to the posterior part of the shell. Scale bar represents 1 cm

Type species: *Spondylus obliquus* von Münster, 1841 (original designation).

Newaagia noetlingi Frech, 1909

? 1833 *Ostrea multicostata* Münster in Goldfuss: 3, pl. 72, fig. 2.

1880 *Hinnites* (*Terquemia*) *comtus* Goldfuss—Noetling: 322, pl. 8, fig. 3.

1909 *Philippiella noetlingi* sp. nov.—Frech: 29–30, pl. 3, figs 1–3.

1915 *Philippiella noetlingi* Frech—Assmann: 595, pl. 31, 1–4.

Description: Shell medium-sized, externally covered with ca. 25 squamose radial ribs (Fig. 7a). Dorsal margin with small auricles (Fig. 7b–c) and central beak projecting beyond plane of commissure (Fig. 7c). Ligament area with broad and shallow resilifer and flat, relatively broad bourrelets.

Remarks: According to Frech (1909), this species has previously been confused with *Ostrea comta* Goldfuss, 1833 (spelling emended as *compta* by Philippi 1898 and subsequent authors), because Bittner (1898, footnote p. 714) reported a byssal notch in "*Hinnites* (*Spondylus*) cfr. *comptus*" from the Anisian of the Dolomites, whereas Noetling's (1880) assignment of this species to *Hinnites* (*Terquemia*?) suggests cementation rather than byssal attachment of the right valve. In consequence, Frech (1909) introduced *Philippiella noetlingi* for the cemented species. The byssally attached species from the Dolomites was subsequently described as *Pseudomorphotis beneckei*

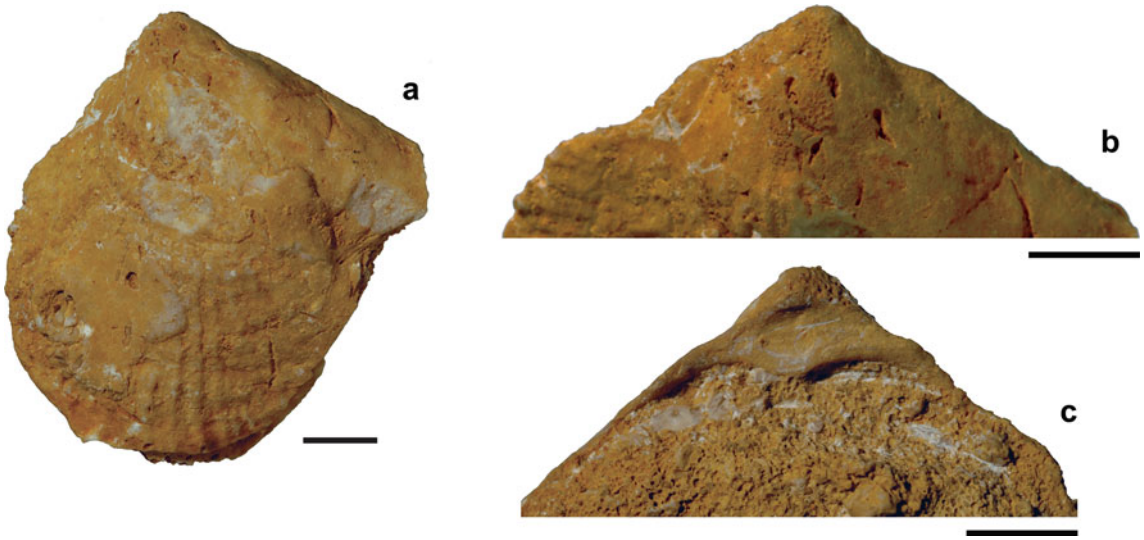

Fig. 7 *Newaagia noetlingi* Frech, 1907, collection of the Muschelkalkmuseum Ingelfingen, MHI 943/16, presumably left valve with some overgrowth. **a** exterior, showing radial ribs, **b** exterior of umbonal region showing auricles, **c** ligament area, showing broad resilifer. *Scale bars* represent 1 cm

Bittner, 1901b, but has recently been reassigned to Goldfuss' species as *Neomorphotis compta* by Posenato (2008). Indeed, the ornament of the species from the Dolomites is very similar to the figure of *Ostrea comta* in Goldfuss (1833, refigured in Fig. 2i), but the presence or absence of a byssal notch in the holotype is unfortunately unknown. Our material differs from *Ostrea comta* in having radial ribs of similar strength rather than sets of intercalating ribs of different strength (compare Fig. 3i with Fig. 7a) and in this respect is similar to Noetling's (1880) material on which *Newaagia noetlingi* has been based.

Ostrea multicostata Münster in Goldfuss, 1833 (fig. 3f) is externally similar to *Newaagia noetlingi* and might represent an older available name. However, in the absence of information on the shell interior, we refrain from formal synonymizing.

Family Ostreidae Rafinesque-Schmaltz, 1815
Genus *Umbrostrea* Hautmann, 2001a
Umbrostrea? sp.
1954 *Alectryonia* sp.—Seilacher, p. 170, fig. 5.

Description. Shell small, bowl-shaped, consistently attached by the left valve according to the criteria of Seilacher (1954). Shell margin with ca. a dozen plicae, abruptly upraising beyond the relatively large attachment area.

Remarks: As noted by Hautmann (2006a), the aragonitic inner shell layer of the described material of this species is generally dissolved, thereby removing all information on internal structures including the ligament area. We attribute this species to *Umbrostrea* based on the cementation by the left valve, the aragonitic mineralogy of the inner shell layer (inferred from its selective dissolution), and the plicate shell margin. Alternatively, the taxon might belong to the recently proposed genus *Narcolopha* Carter and Malchus (in Carter et al. 2011). Because of the incomplete preservation of the available material, we describe this species in open nomenclature.

Although the examined specimens are smaller and have a relatively larger attachment area than *Noetlingiconcha speculostreum*, mixing up of both species might have occurred because of the similarity of their ornaments. The small shell size, relatively large attachment area and steeply upraising shell margin may collectively be related to the mode of life as epizoans on the limid bivalve *Plagiostoma*, which limits growth space. We suppose that under comparable substrate conditions, valve orientation would remain the sole criterion for distinguishing this earliest known oyster species from the stratigraphically co-occurring *N. speculostreum*.

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References

Aberhan, M., and H. Muster. 1997. Palaeobiology of early Jurassic bakevelliid bivalves from western Canada. *Palaeontology* 40(3): 799–815.

Assmann, P. 1915. Die Brachiopoden und Lamellibranchiaten der oberschlesischen Trias. *Jahrbuch der preußischen Geologischen Landesanstalt* 34(1): 586–638.

Bachmann, G.H. 1973. Die karbonatischen Bestandteile des Oberen Muschelkalkes (Mittlere Trias) in Südwest-Deutschland und ihre Diagenese. *Arbeiten aus dem Institut für Geologie und Paläontologie der Universität Stuttgart, Neue Folge* 68: 1–99.

Bittner, A. 1898. Beiträge zur Paläontologie, insbesondere der triadischen Ablagerungen centralasiatischer Hochgebirge. *Jahrbuch der k. k. geologischen Reichsanstalt* 48: 689–718.

Bittner, A. 1901a. Lamellibranchiaten aus der Trias des Bakonyer Waldes. *Resultate der wissenschaftlichen Erforschung des Balatonsees, Anhang: Palaeontologie der Umgebung des Balatonsees* 2(3): 1–107.

Bittner, A. 1901b. Ueber Pseudomonotis Telleri und verwandte Arten der unteren Trias. *Jahrbuch der k.k Geologischen Reichsanstalt* 50: 559–592.

Busse, E. 1972. Fazies und Fauna des Oberen Muschelkalkes von Willebadessen. *Philippia* 1(3): 110–126.

Carter, J.G., C.R. Altaba, L.C. Anderson, R. Araujo, A.S. Biakov, A.E. Bogan, D.C. Campbell, M. Campbell, Jin-hua Chen, J.C.W. Cope, G. Delvene, H.H. Dijkstra, Zong-jie Fang, R.N. Gardner, V.A. Gavrilova, I.A. Goncharova, P.J. Harries, J.H. Hartman, M. Hautmann, W.R. Hoeh, J. Hylleberg, Bao-yu Jiang, P. Johnston, L. Kirkendale, K. Kleemann, J. Koppka, J. Kříž, D. Machado, N. Malchus, A. Márquez-Aliaga, J.-P. Masse, C.A. McRoberts, P.U. Middelfart, S. Mitchell, L.A. Nevesskaja, S. Özer, J. Pojeta Jr., I.V. Polubotko, J.M. Pons, S. Popov, T. Sánchez, A.F. Sartori, R.W. Scott, I. I. Sey, J.H. Signorelli, V.V. Silantiev, P.W. Skelton, T. Steuber, J.B. Waterhouse, G.L. Wingard, T. Yancey. 2011. A synoptical classification of the Bivalvia (Mollusca). *Paleontological Contributions* 4: 1–47.

Checa, A.G., A.P. Jiménez- Jiménez, A. Márquez-Aliaga, and H. Hagdorn. 2006. Further comments on the origin of oysters. *Palaeogeography, Palaeoclimatology, Palaeoecology* 240: 672–674.

Chrząstek, A. 2002. Stratygrafia i warunki sedymentacji retu oraz dolnego wapienina muszlowego niecki północnosudeckiej. *Prace geologiczno-mineralogiczne* 73: 1–128.

Cox, L.R. 1969. Family Terquemiidae Cox, 1964. In *Treatise on invertebrate paleontology. Part N. Mollusca 6, Bivalvia 1*, ed. R.C. Moore, N380-N382. Boulder, Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas Press.

Dall, W.H. 1895. Tertiary mollusks of Florida. Part 3. A new classification of the Pelecypoda. *Transaction of the Wagner Free Institute of Science of Philadelphia* 3(3): 483–565.

de Lamarck, J.B. 1809. *Philosophie zoologique, ou, Exposition des considérations relative à l'histoire naturelle des animaux*. Paris: Dentu.

Deshayes, G.P. 1832. *Encyclopédie méthodique. Histoire naturelle des vers. Tome 2.* Paris: Agasse.

Diener, C. 1923. Lamellibranchiata triadica. *Fossilium catalogus I: Animalia. Pars 19*. 257 p. Berlin: W. Junk.

Frech, F. 1909. Die Leitfossilien der Wefener Schichten und Nachträge zur Fauna des Muschelkalkes der Cassianer und Raibler Schichten sowie des Rhaet und des Dachsteinhauptdolomites (Hauptdolomit). *Resultate der wissenschaftlichen Erforschung des Balatonsees, Anhang: Palaeontologie der Umgebung des Balatonsees* 1(1): 1–95.

Fürsich, F.T., and J. Wendt. 1977. Biostratinomy and palaeoecology of the Cassian formation (Triassic) of the southern Alps. *Palaeogeography, Palaeoclimatology, Palaeoecology* 22: 257–323.

Giebel, C. 1856. *Die Versteinerungen im Muschelkalk von Lieskau bei Halle*. Berlin: Verlag von Karl Wiegandt.

Giribet, G., and W.C. Wheeler. 2002. On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. *Invertebrate Biology* 121: 271–324.

Giribet, G., and D.L. Distel. 2003. Bivalve phylogeny and molecular data. In *Molecular systematics and phylogeography of Mollusks*, ed. C. Lydeard, and D.R. Lindberg, 45–90. Washington, D.C.: Smithsonian Institution Press.

Goldfuss, G.A. 1833. *Petrefacta Germaniae. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angrenzenden Länder. Unter Mitwirkung des Herrn Grafen Georg zu Münster.* 2. Theil, 4. Lieferung. 1–68, pls 72–96. Düsseldorf: Arnz & Co.

Goldfuss, G.A. 1863. *Petrefacta Germaniae. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angrenzenden Länder. Unter Mitwirkung des Herrn Grafen Georg zu Münster.* 2. Theil. 2. edition; 298 p., pls 72–165. Leipzig: List & Francke.

Hagdorn, H. 1978. Muschel/Krinoiden-Bioherme im Oberen Muschelkalk (mo1, Anis) von Crailsheim und Schwäbisch Hall (Südwestdeutschland). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 156(1): 31–86.

Hagdorn, H., and W. Ockert 1993. *Encrinus liliiformis* im Trochitenkalk Süddeutschlands. In *Muschelkalk. Schöntaler Symposium 1991* (=*Sonderbände der Gesellschaft für Naturkunde in Württemberg 2*), eds. H. Hagdorn and A. Seilacher, 245–260. Korb: Goldschneck.

Hautmann, M. 2001a. Taxonomy and phylogeny of cementing Triassic bivalves (Families Prospondylidae, Plicatulidae, Dimyidae and Ostreidae). *Palaeontology* 44(2): 339–373.

Hautmann, M. 2001b. Die Muschelfauna der Nayband-Formation (Obertrias, Nor-Rhät) des östlichen Zentraliran. *Beringeria* 29: 1–181.

Hautmann, M. 2004. Early Mesozoic evolution of alivincular bivalve ligaments and its implications for the timing of the "Mesozoic marine revolution". *Lethaia* 37: 165–172.

Hautmann, M. 2006a. Shell mineralogical trends in epifaunal Mesozoic bivalves and their relationship to seawater chemistry and atmospheric carbon dioxide concentration. *Facies* 52: 417–433.

Hautmann, M. 2006b. Shell morphology and phylogenetic origin of oysters. *Palaeogeography, Palaeoclimatology, Palaeoecology* 240: 668–671.

Hautmann, M., and M. Golej. 2004. *Terquemia* (*Dentiterquemia*) *eudesdeslongchampsi* new subgenus and species, an interesting cementing bivalve from the Lower Jurassic of the western Carpathians (Slovakia). *Journal of Paleontology* 78(6): 1086–1090.

Hertlein, L.G. 1952. Newaagia, a new name for Philippiella Waagen. *Journal of Paleontology* 26: 275.

Krumbeck, L. 1913. Obere Trias von Buru und Misol. *Palaeontographica, Supplement-Band* 4: 1–161.

Kutassy, A. 1931. Lamellibranchiata triadica. In: *Fossilium catalogus I: Animalia. Pars 51,* ed. W. Quenstedt, 261–475. Neubrandenburg: Gustav Feller.

Lukas, V. 1992. Zur Diagenese der Karbonate des Unteren Muschelkalk (Trias). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 185(1): 85–113.

Malchus, N. 2004. Early ontogeny of Jurassic bakevelliids and their bearing on bivalve evolution. *Acta Palaeontologica Polonica* 49(1): 85–110.

Márquez-Aliaga, A., A.P. Jiménez- Jiménez, A.G. Checa, and H. Hagdorn. 2005. Early oysters and their supposed Permian ancestors. *Palaeogeography, Palaeoclimatology, Palaeoecology* 229: 127–136.

Matsumoto, M. 2003. Phylogenetic analysis of the subclass Pteriomorphia (Bivalvia) from mtDNA COI sequences. *Molecular Phylogenetics and Evolution* 27: 429–440.

Morris, J., and J. Lycett. 1853. A monograph of the Mollusca from the Great Oolite, chiefly from Minchinhampton and the coast of Yorkshire, part II, Bivalves. *Palaeontographical Society London* 7(23): 1–80.

Münster, G. von. 1841. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. In *Beiträge zur Petrefaktenkunde*, II, eds. Wissmann H.L., and G. von Münster, 68–152. Bayreuth: Buchner′sche Buchhandlung.

Muster, H. 1995. Taxonomie und Paläobiogeographie der Bakevelliidae (Bivalvia). *Beringeria* 14: 1–161.

Newell, N.D., and D.W. Boyd. 1970. Oyster-like Permian Bivalvia. *Bulletin of the American Museum of Natural History* 143(4): 217–282.

Niedzwiedzki, R. 2000. Litostratygrafia formacji górazdzanskiej I formacji dziewkowickiej na Slasku Opolskim. *Prace Geologiczno-Mineralogiczne* 71: 1–72.

Noetling, F. 1880. Die Entwicklung der Trias in Niederschlesien. *Zeitschrift der deutschen geologischen Gesellschaft* 32, 300–349, pls 13–15.

Philippi, E. 1898. Beiträge zur Morphologie und Phylogenie der Lamellibranchier. *Zeitschrift der deutschen geologischen Gesellschaft* 50: 597–622.

Philippi, E., and F. Frech. 1903. Die wirbellose Meeresfauna der deutschen Trias. In *Lethaea geognostica. Handbuch der Erdgeschichte mit Abbildungen der für die Formationen bezeichnendsten Versteinerungen. II. Theil, Das Mesozoicum. 1. Heft, Die Trias. 1. Lieferung*, ed. F. Frech, 25–29. Stuttgart: Schweizerbart.

Posenato, R. 2008. Anisian (Middle Triassic) bivalves from the Dolomites (Italy). *Neues Jahrbuch für Geologie und Paläontologie* 247(1): 93–115.

Ptschelinceva, G.T. 1960. Family Prospondylidae fam. nov. In *Fundamentals of palaeontology. Molluscs-Loricata, Bivalvia, Scaphopoda,* ed. A.G. Eberzin, 86–87. Moscow: Isdatel'stvo Akademii Nauk SSSR (in Russian).

Rafinesque-Schmaltz, C.S. 1815. *Analyse de la nature ou tableau de l′Univers et des corps organisés*. Palermo: Jean Barravecchia.

Röhl, U. 1988. *Multistratigraphische Zyklengliederung im Oberen Muschelkalk Nord- und Mitteldeutschlands.* 285 p. PhD Thesis Rheinische Friedrich-Wilhelms-Universität Bonn.

Römer, F. 1851. Ueber einige neue Versteinerungen aus dem Muschelkalke von Willebadessen. *Palaeontographica* 1: 311–315.

Schmidt, M. 1928. *Die Lebewelt unserer Trias*. Öhringen: Hohenlohesche Buchhandlung F. Rau.

Seilacher, A. 1954. Ökologie der triassischen Muschel *Lima lineata* (Schloth.) und ihrer Epöken. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1954(4): 163–183.

Seilacher, A. 1984. Constructional morphology of bivalves: Evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology* 27: 207–237.

Steiner, G.A., and S. Hammer. 2000. Molecular phylogeny of the Bivalvia inferred from 18S rDNA sequences with particular reference to the Pteriomorphia. In: *Evolutionary Biology of the Bivalvia,* eds. E.M. Harper, J.D. Taylor, and J.A. Crame, 11–29. London: Geological Society, Special Publications 177.

Stenzel, H.B. 1971. Oysters. In *Treatise on invertebrate paleontology. Part N. Mollusca 6, Bivalvia 1*, ed. R.C. Moore, N953-N1224. Boulder, Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas Press.

Tate, R. 1868. *Appendix to the Manual of Mollusca of S. P. Woodwards, A.L.S., containing such recent and fossil shells as are not mentioned in the second edition of that work.* London: Virtue & Co.

von Klipstein, A. 1843. *Beiträge zur geologischen Kenntnis der östlichen Alpen*. Gießen: Heyer.

von Schlotheim, E.F. 1820. *Die Petrefactenkunde auf ihrem jetzigem Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert*. Beckersche Buchhandlung: Erste Abtheilung. Das Thierreich. Gotha.

von Schlotheim, E.F. 1823. *Nachträge zur Petrefactenkunde. Zweyte Abtheilung*. Gotha: Beckersche Buchhandlung.

Waagen, L. 1907. Die Lamellibranchiaten der Pachycardientuffe der Seiser Alm nebst vergleichend paläontologischen und phylogenetischen Studien. *Abhandlungen der k.k. geologischen Reichsanstalt* 18(2): 1–180.

Zeeh, S., and H. Hagdorn. 2002. Taphonomie von Muschelkalk-Cephalopoden. Teil 2: Diagenese (Zementation und Kompaktion). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 223(3): 351–376.